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The Functional Significance of the Hypocercal Tail and Lateral Fin Fold of Anaspid Ostracoderms

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The Anaspida are Silurian and Devonian jawless fishes which are unique among aquatic vertebrates in possessing a well-developed hypocercal tail in combination with elongate paired fins (or fin folds) extending from just behind the branchial region to the level of the anal fin. In the hypocercal type of tail the notochordal axis bends downward and supports an enlarged fin (epichordal lobe) on its upper surface. It is assumed that as such a tail moved from side to side through the water, the more flexible dorsal lobe of the caudal fin would be passively bent, thus giving it an angle of attack which would create a downward as well as a forward (propulsive) and transverse (drag) force on the tail. The downward force would depress the tail end of the body and consequently create a positive (upward) pitch of the head end. Until recently, it was thought that the hypocercal type of tail was correlated with the absence of paired fins (e.g., Affleck, 1950), but Ritchie (1964) has shown that paired fin folds were probably present in all anaspids. Miles (in Moy-Thomas and Miles, 1971) and Thomson (1971) have recently commented on the possibility of a functional relationship between the fin fold and hypocercal tail of anaspids, though both point out that the significance of the combination is not yet understood. The purpose of this paper is to suggest how the fin fold and hypocercal tail of Anaspida were hydrodynamically related to one another.

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The analysis presented here applies only to the Anaspida, for only in this group of ostracoderms is there good evidence that the tail was truly of the hypocercal type, that is, that the notochordal axis did indeed extend into the ventral lobe. The tail of the Pteraspida may not have been truly hypocercal because the position of the notochord within the tail is not known (Denison, 1971). Indeed, Aleev (1963) has analyzed the tail of *Pteraspis* as though it generated an upward rather than a downward force. Likewise, the supposed hypocercal tail of the Thelodonti is too poorly known to be sure that it functioned as a true hypocercal tail.

THE ACTION OF HETEROCERCAL AND HYPOCERCAL TAILS

No living fish possesses a true hypocercal tail, but current views of its functional significance have come from numerous experimental studies of the function of the heterocercal type of tail which characterizes living sharks and the primitive members of all groups of gnathostome fishes. Several experimental studies using models of hypocercal tails (Grove and Newell, 1936; Kermack, 1943; Affleck, 1950) have yielded results which support the functional conclusions based on analyses of heterocercal tails.

In the heterocercal type of tail the notochordal axis bends upward and supports an enlarged fin (hypochordal lobe) on its undersurface. Numerous studies (e.g., Harris, 1936; Alexander, 1965) have demonstrated that the heterocercal tail of sharks produces lift at the posterior end of the body and negative (downward) pitch at the head end. This negative pitch is balanced by lift at the front end generated by the pectoral fins and flattened ventral surface of the head and trunk. The total lift has the important effect of equalizing the downward force due to the weight of the shark (which is usually heavier than water) and so counters the tendency of the fish to sink to the bottom (fig. 1A). As a consequence of these analyses, it has been widely assumed that the adaptive significance of the heterocercal tail lies in its ability to generate lift in negatively buoyant fishes. It has also been assumed that such a tail can function "properly" only in combination with paired pectoral fins which are required to counteract the negative pitch produced by the tail.

Applying these lines of reasoning to a consideration of the functional significance of the hypocercal tail has led to a great emphasis being placed on the downward component of the tail thrust (Harris,

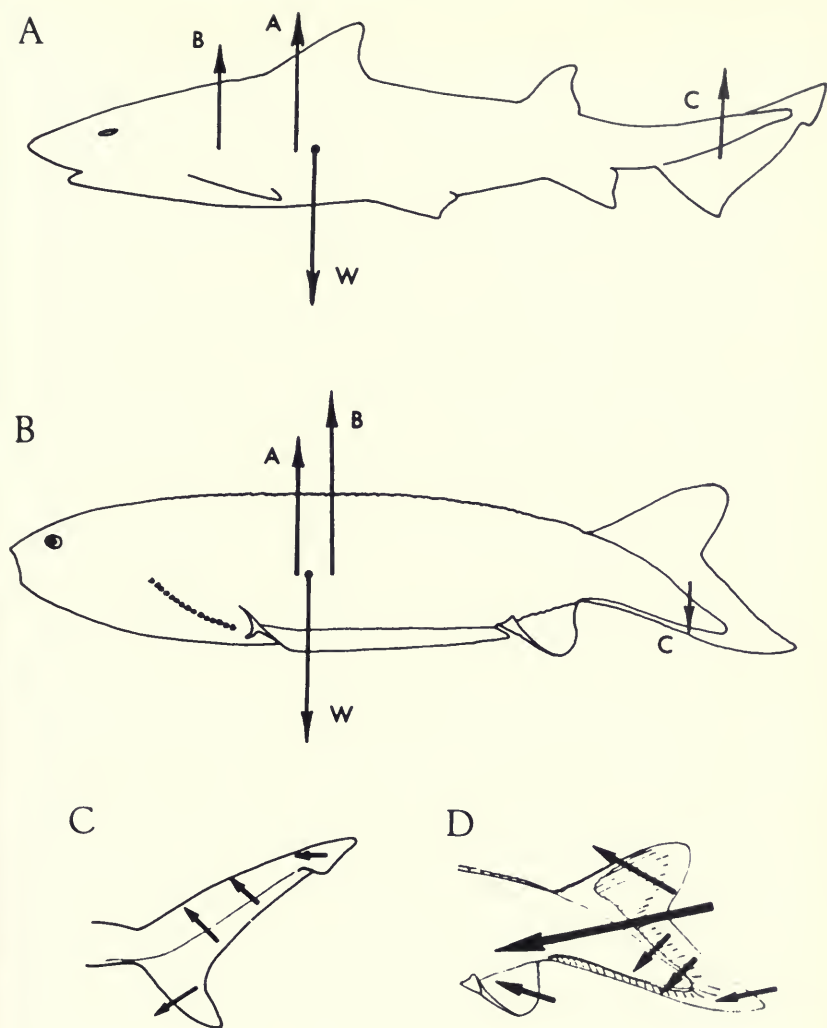


Fig. 1. A. The vertical forces acting on a shark swimming horizontally. B. The vertical forces acting on the anaspid *Pharyngolepis oblongus* swimming horizontally. C. Suggested directions of thrusts developed by different parts of the tail of a shark. D. Suggested directions of thrusts developed by the anal fin and different parts of the caudal fin of an anaspid (small arrows) and suggested resultant thrust of the anal plus caudal fins (heavy arrow). See text for explanation of the symbols. In all figures, the lengths of the arrows are not intended to represent exact magnitudes. A modified from Alexander (1965) and Thomson (1971). B and D based on a reconstruction by Ritchie (1964). C from Thomson (1971).

1936; Kermack, 1943; Affleck, 1950). It has been assumed that in forms which were heavier than water and which lacked pectoral fins, the lift required for free swimming was generated by the undersurface of the front part of the body moving forward through the water at a positive angle of pitch. The function of the hypocercal tail was to raise the front end to the necessary positive angle by depressing the posterior end. However, as pointed out by Kermack (1943), such fishes had the problem of balancing the positive pitching moments produced by both the tail and the head, for without the means of producing compensatory negative pitching moments these fishes would be incapable of achieving equilibrium while swimming. Kermack assumed that pteraspids were in pitching equilibrium because the heavy armor on the front part of the body caused the center of gravity to lie anterior to the center of buoyancy and thereby produce a negative pitching moment equal to the sum of the positive moments. For anaspids, which lacked heavy armor, Harris (1936) suggested that equilibrium was achieved by the fish swimming at the surface with its head end just "awash" so that the extra weight of this region out of water might produce a negative pitching moment sufficient to compensate for the positive moment produced by the tail. Although anaspids may have been surface feeders, this method of achieving equilibrium in pitch is extremely unlikely inasmuch as it implies that these fishes lacked effective control over pitching instability in all other situations.

The above hypotheses suggest that those ostracoderms possessing hypocercal tails maintained pitching equilibrium by adjusting the speed and the angle of attack of the body so that lift created by its ventral surface just balanced the downthrust of the tail plus the sinking tendency due to the weight of the fish. In the case of anaspids, where swimming must have been at higher speeds than in pteraspids, the hydrodynamic instability of such methods of maintaining pitching equilibrium would have been very great. However, anaspids did possess paired fins, albeit of a unique type for vertebrates, and it seems certain that these fins must have functioned in the maintenance and adjustment of pitching equilibrium as do the pectoral fins of those fishes with a heterocercal tail. The problem, then, is to determine how the fin fold accomplished these functions.

Thomson (1971) has recently presented an analysis of the action of heterocercal tails in which he develops concepts which are useful in interpreting hypocercal tails as well. His main conclusion, earlier reached by Aleev (1963), is that the upward and downward forces

produced in a heterocercal tail may under certain conditions be balanced so that they cancel out, leaving only a forward thrust. Thus, morphologically heterocercal tails could be evolved which are capable of producing epibatic, isobatic, and even hypobatic (upward, level, or downward) movement. Furthermore the evolution of active control of the profile of the tail fin by differential action of radial musculature acting on skeletal supports could allow the fish to adjust the hydrodynamic characteristics of the tail to changes in speed and other factors (see Alexander, 1965). This point is also stressed by Simons (1970) whose experiments on the tails of certain sharks have demonstrated that the prominent ventral hypochordal lobe (fig. 1C) is capable of reducing the net lift of the heterocercal tail by producing a downward rather than an upward force. This occurs because the thicker anteroventral edge of the lobe resists lateral bending so that only the thinner posterodorsally-facing portion of the lobe is bent and thus generates a forward and downward reaction force (fig. 1C). This force partially counteracts the upward force generated by the flexible longitudinal hypochordal lobe (fig. 1C) on the underside of the more rigid upturned notochordal axis of the tail. A point of major difference between Simons' study and those of most earlier workers is that the hypochordal portion of the caudal fin does not behave as a passively trailing flap below the leading edge of the notochordal axis and, as a result, does not produce wholly upwardly-directed vertical forces.

The studies of Simons and Thomson suggest a new way of viewing the hydrodynamic characteristics of the hypocercal tail of the Anaspida. Where adequately known, the anaspid tail always possesses a prominent dorsal epichordal lobe separated from a more posterior low longitudinal epichordal lobe by a distinct emargination (fig. 1D). In *Pharyngolepis oblongus*, where the tail is well-preserved, the anterodorsal and anteroventral part of the large epichordal lobe is covered with small scales while the more posterior and distal part of the fin is supported by dermal fin rays (Ritchie, 1964). Furthermore, Jarvik (1959) has convincingly demonstrated that the fins of anaspids contained endoskeletal radials extending to their outer edges which were probably moved by radial muscles at the bases of the fins. These observations suggest that the large epichordal lobe was thicker and stiffer anteriorly than it was posteriorly, so that bending due to transverse movements of the entire tail was restricted to the posteroventrally-facing trailing edge of the lobe. Consequently, it is probable that the dorsal epichordal lobe pro-

duced an upward rather than downward force; that is, it acted like the large hypochordal lobe in the tail of certain sharks (fig. 1C) though in the opposite direction.

The possible forces produced by the different parts of the tail of *Pharyngolepis* are illustrated in Figure 1D. Also included is the force produced by the anal fin which is stiffened anteriorly by a stout fin-spine. The long arrow indicates the probable direction of the resultant thrust developed by the caudal plus anal fins. Its low angle is consistent with Simons' experimental results on the similarly-shaped heterocercal tail of the Port Jackson shark, *Heterodontus*. The conclusion which this admittedly rough analysis suggests is that the propulsive organ (caudal plus anal fins) of the anaspids produced a thrust with a large horizontal component contributing to forward locomotion and a relatively small, though hydrodynamically important, vertical component tending to depress the tail. Though the tail appears to be functionally hypobatic, it is possible that it could have been nearly or actually isobatic in some anaspids (see below).

ANALYSIS OF VERTICAL FORCES ACTING ON ANASPIDS

Having concluded that the net downward force acting on the anaspid tail was probably much smaller than formerly thought, I shall now attempt to analyze all of the vertical forces acting on a horizontally-swimming anaspid in the same way that Alexander (1965) has analyzed the vertical forces acting on a shark (fig. 1A, B).

In order for a fish to be in equilibrium while swimming horizontally, the following conditions must be met: (1) upward forces acting on the fish must equal downward forces; and (2) turning moments must equal zero. In the case of the shark (fig. 1A), the fish's weight (W) acting through its center of gravity is balanced by the upthrust of the water the fish displaces (A) acting through its center of buoyancy, plus the lift produced by the pectoral fins and snout (considered together as B) and by the tail (C). Thus,

$$W = A + B + C.$$

Balancing the moments anterior and posterior to the center of gravity, taking a , b , and c as the distances from the center of gravity of A , B , and C , we find that

$$Aa + Bb = Cc.$$

For an anaspid (fig. 1B) I have chosen *Pharyngolepis oblongus* because it is perhaps the best-known anaspid thanks to the recent description by Ritchie (1964). The approximate center of gravity was obtained from a life-sized clay model based on Ritchie's figures; it lies a short distance behind the leading edge of the lateral fin fold so that only about one-eighth of the fin lies in front of it. The center of buoyancy cannot be determined, but the lightly-armored anaspids may have resembled sharks in having it slightly in front of the center of gravity (Alexander, 1965); this case would represent the least favorable of possible alternatives. The lift generated by the paired fin folds is assumed to act about one-quarter of the distance along the length of the fin because the center of lift of a typical airfoil is near the 25 per cent point along its chord (Magnuson, 1970). By convention, the lifting area of a wing or fin includes not only the exposed area of the wing but also the area through the body between the wings (Magnuson, 1970); therefore, the area through that portion of the trunk between the paired fin folds is added to the area of the fins. This total area is considered to have produced the lift designated as B. Because anaspids were relatively fusiform fishes, the lift provided by the rounded undersurface of the head and pharyngeal region was probably very slight and is not considered here.

Balancing the vertical forces, we find that

$$W + C = A + B.$$

The downthrust of the hypocercal tail adds to the sinking tendency caused by the weight of the fish; the lift generated by the fin folds is an important force countering both downward forces. The magnitude of the upward thrust produced by the fin folds would vary with the forward speed and with the inclination of the fins in the pitching plane, i.e., with their angle of attack. Both of these factors would vary in relation to the magnitude and direction of the total thrust produced by the tail.

Balancing the turning moments about the center of gravity, we have

$$Aa + Cc = Bb.$$

From this, we see that only the fin fold contributes to the negative

pitching force required to balance the positive pitching forces. Of these, A lies very close to the center of gravity, so that C is the principal positive pitching force which must be countered by B. Because the distance b is very small relative to distance c , it follows that the magnitude of C would have to be very small relative to B in order for pitching moments to equal zero. This is consistent with the interpretation that the vertical component of the thrust produced by the anaspid tail was small.

DISCUSSION

This analysis leads to the conclusion that the primary function of the anaspid fin fold was to provide an upthrust to balance the combined downthrusts produced by the body weight and the hypocercal caudal fin. In order to do this the upthrust had to act *between* the center of gravity and the tail. This explains why the fin fold extends back to the anal fin but forward only slightly anterior to the midregion of the trunk. Ritchie (1964) suggested that the lateral fins of anaspids increased pitching plane stability by increasing positive pitch, but this is precisely what an anaspid would not need. Increasing positive pitch would have increased the rotational moments about the center of gravity and, thus, the tendency for the fish to swim in a series of loops. Equilibrium in the pitching plane would be achieved only by increasing negative pitch, and this is what the fin fold, because of its position, was adapted to do.

The analysis also explains why the paired fins of anaspids are, with at least one known exception (see below), greatly elongated, extending over one-third the length of the trunk. The fin folds provide the only upthrust against the downthrust of the caudal fin so that the farther they extend behind the center of gravity, the more effective they will be in balancing the vertical thrust created by the tail. Also, because lift forces are directly related to the area of the lifting surface, a long fin will provide greater lift than a short one of equal lateral extent. A shorter fin of greater lateral extent would be an equally effective means of providing sufficient negative pitch to counter the positive pitch produced by the tail. However, the fin fold has the additional function of providing the lift required to equalize the sinking tendency caused by the weight of the fish, consequently the most stable situation is one in which the lift is centered relatively close behind the center of gravity rather than a great distance behind it. Therefore, the anterior end of the fin fold should lie somewhat in front of the center of gravity. It was noted

above that the ventral surface of the trunk between the paired fins added to the total lift so that the short lateral extent of the fin fold was probably sufficient to satisfy the requirements for a stabilizing lift-producing mechanism.

I conclude that the elongate fin fold which characterized most anaspids was the result of a compromise between the requirements for: (1) generating sufficient lift to counter sinking forces and maintain horizontal equilibrium; and (2) spreading the lift force over a large antero-posterior portion of the trunk in order to increase dynamic stability.

It should be noted that the fin fold of anaspids, because of its concentration behind the center of gravity, was capable of correcting any positive pitching action of the hypocercal tail in a *passive* manner because increased positive pitch automatically increased the angle of attack of the paired fins and the lift they produced. Thus, the fin fold-hypocercal tail system of anaspids made these fishes hydrodynamically stable in the pitching plane. The pectoral fin-heterocercal tail system of sharks and various primitive fishes does not possess such hydrodynamic stability; constant adjustment of the angle of attack of the pectorals is required in order to control pitching. However, the very instability of the pitch-adjusting system of shark-like fishes means that these fishes possess great maneuverability. It may be concluded that anaspids possessed limited maneuverability as compared with a typical gnathostome fish. Nevertheless, because the caudal and paired fins of anaspids were probably under some muscular control (Jarvik, 1959; Ritchie, 1964), it is likely that the orientation and stiffness of different parts of the fins could be differentially modified to vary the direction and magnitude of the forces they produced. In this way the equilibrium orientation of the fish could be modified for turning, rising, or descending, or for swimming in a stable heads-up or -down position.

The possibility that a hypocercal tail could become functionally isobatic is indicated by *Pharyngolepis heintzi* (Ritchie, 1964), in which the fin fold is shortened so as to correspond only to the anterior half of the fin fold of *P. oblongus*. The fin is roughly triangular in outline, with an angulation at its widest point about one-third of the distance from its leading edge. Comparison with *P. oblongus* suggests that the broadest part of the fin lay approximately below the center of gravity. Elimination of the posterior half of the typical anaspid fin fold in *P. heintzi* means that the center of the lift force which the fin produced lay much closer to the center of gravity than

it did in *P. oblongus*. It also means that the amount of lift force available for countering any downward thrust produced by the tail was practically nil. The tail of *P. heintzi* is not known, but I conclude that it must have been nearly or actually isobatic; that is, the thrust it produced must have passed directly through, or perhaps very slightly below, the center of gravity. Only under these conditions could such a short, anteriorly-located fin be sufficient to balance any positive forces acting on the fish. The main functions of such a short fin fold would be to provide lift needed to counter the sinking tendency due to the weight of the fish and to provide maneuverability in the pitching and rolling planes. The shorter fin undoubtedly decreased the dynamic stability of the fish, but it simultaneously increased maneuverability. However, because the fin lay directly below the center of gravity, any turning moments which it produced would have been extremely small and could readily have been balanced by slight adjustments of the caudal fin. In this respect, *P. heintzi* has converged to a great extent on such higher teleosts as gobies and stargazers in which the relatively large pectoral fins lie close to the center of gravity and produce very small or no turning moments (Aleev, 1963).

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